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Oligochaetes

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I. Introduction

As long ago as 1789, Gilbert White of Selborne appreciated that earthworms contribute considerably to the fertility of soil by their mode of burrowing and feeding. Just under a century later Charles Darwin (1881) in his book, "The Formation of Vegetable Mould through the Action of Worms", showed that they play an important role in the disappearance of surface plant litter, its breakdown and incorporation within the soil. Since Darwin's time, especially in recent years, much work has been done to evaluate more precisely the part played by oligochaetes, particularly earthworms, in plant litter breakdown. Today, the role of oligochaetes in plant litter breakdown is seen as a complex one, with many factors involved. There is still much work to be done before the subject is completely understood.

II. Types of Oligochaetes Involved

A. Enchytraeidae

These are very small, pale-coloured worms, commonly known as pot worms. They are small compared with the Lumbricidae, with which this chapter is mainly concerned. The largest species grow up to 5 cm long, but the majority of species are 1 cm or less in length. They are found in soils in large numbers, especially in acid soils with a high organic matter content. O'Connor (1957) has recorded up to 250,000 m^{-2} in a coniferous forest soil, and Peachey (1963) 300,000 m^{-2} in a *Juncus* moorland soil. Despite the large numbers that can occur in some soils, the biomass is considerably less than most lumbricid populations. For example, in Peachey's *Juncus* moorland site, the biomass was only 53 g m^{-2}.

B. Lumbricid Earthworms

Lumbricid earthworms are the most important group of terrestrial oligochaetes involved in litter breakdown and turnover, particularly in temperate soils, as it is within the temperate zones that they are most widely distributed. They are the dominant oligochaete family, especially in those areas cultivated by man. It is in temperate soils, therefore, that earthworms contribute most to litter breakdown and turnover. Edwards and Heath (1963) considered that they may be responsible for up to 78% of the total litter disintegration.

Lumbricid earthworm species can be subdivided into 3 groups according to their feeding and burrowing activities: (a) surface feeding, (b) surface casting, and (c) other species that do not, to any extent, do either.

1. Surface Feeders

Lumbricus terrestris (Linn.) is undoubtedly the most important species in this group. Although a certain amount of nutrient is obtained from soil passing through the gut during burrowing activities, most food material is obtained from surface litter. The food material is foraged from an area around the mouth of the burrow, and is pulled into the burrow so as to form a plug at the mouth. Feeding then takes place upon the stored material. The material pulled down depends upon what is available, but, generally, only material that has become detached from growing plants is used.

L. terrestris is not the only surface feeder in temperate areas, but other species make more limited forays, and their contribution to the removal of surface litter is small.

2. Surface Casting Species

Some lumbricid species void their excreta onto the soil surface, rather than within the soil structure or onto the walls of their burrows. Species responsible for much of the surface casting include *Allolobophora longa* (Ude), *A. nocturna* Evans, and *A. caliginosa* (Sav.), and several others also do so to some extent. *L. terrestris* also casts on the surface on occasion. Casts are produced in greatest numbers during spring and autumn months.

Many authors have calculated the amounts of cast material brought to the surface by such species during one year. Darwin (1881) estimated that up to 40 t ha^{-1} were produced annually in English pasture, Guild (1951) 27 t ha^{-1} also in England, and Stockli (1949) 100 t ha^{-1} in Zurich, Switzerland.

3. Underground Feeding and Casting Species

These constitute the majority of lumbricid species. Evans (1948) assumed that, in English pasture, the weight of cast material produced by species within the soil was (weight for weight) at least equal to that voided by casting species on the surface. He calculated that in pasture fields at Rothamsted, up to 82 t ha^{-1} of total cast material was ejected by earthworms per annum. He also calculated that the top 10 cm of soil of a densely populated pasture field would pass through the guts of the earthworms in $11\frac{1}{2}$ years, although in an arable field with a low earthworm population it would take up to 80 years.

C. Other Terrestrial Oligochaetes

Although members of the Lumbricidae dominate the temperate areas of the globe, in tropical and sub-tropical regions the terrestrial oligochaetes are represented by other families, such as the Eudrilidae in tropical and subtropical Africa; the Glossoscolecidae, dominant in Central and South America and also represented in North Africa and Southern Europe; and the Megascolecidae, found particularly in East and South-east Asia, and Australasia. Some species of this last family, particularly those of the genus

Pheretima, are widely distributed throughout the world, often competing with the Lumbricidae. Many members of these tropical and sub-tropical families are surface casting species producing very large casts. Lumbricids rarely produce casts weighing more than 100 g, but, in Africa, *Dichogaster jaculatrix* (Octochaetidae) produce casts 10–12 cm high and 4 cm in diameter, and the very large *Notoscolex* earthworms in Burma produce casts up to 25 cm high, one of which Gates (1961) found to weigh 1·6 kg.

III. Populations in Different Habitats

Earthworm populations vary greatly in numbers according to their habitats (Table I). Unfortunately, no method of sampling gives a completely satisfactory quantitative result. Hand-sorting gives a very good estimate of those species living near the surface and among the litter layers and vegetation root system. It is, however, very inaccurate for *L. terrestris*; this species can be extracted very efficiently by the application of dilute formalin to the soil surface, but this method is less suitable for other species. However, the figures given in Table I provide some indication of relative populations. There are many fewer earthworms in moorland and mor than in fertile soils, and the build-up of organic matter on the surface of the former habitats is partly due to the lack of earthworms. Fallow soils also have comparatively few earthworms.

Earthworm populations in arable land are very variable. Arable soils with a high organic content can support quite large populations (Reynoldson *et al.*, 1955). The biomass is low, but this is probably due to the lack of *L. terrestris* in the samples, because of the sampling method used. The sites that support the largest populations are those that provide earthworms with an abundant food supply, such as orchards under grass, pasture lands, and where local aggregations of organic matter occur (e.g. under pig litter). Woodlands on mull soils usually support rather lower populations than pastures, but the biomass may be higher as there are often many *L. terrestris* individuals feeding on the abundant surface litter.

There is comparatively little information on the populations of earthworms in tropical habitats. Block and Banage (1968), using formalin, sampled a range of habitats, including swamp forest, bush, coffee and banana plantations and arable fields in Uganda, and recorded mean numbers of worms (families Acanthodrilidae and Eudrilidae) ranging from 101·8 m^{-2} (banana plantation) to 7·4 m^{-2} (swamp forest). Madge (1969) has recorded 33 m^{-2} in Nigerian grassland, and El-Duweini and Ghabbour (1965) reported mixed populations of lumbricids and non-lumbricids ranging from 8 to 788 m^{-2} from a variety of cultivated or semi-cultivated habitats in Egypt.

Table I. Populations of earthworms in different habitats

	Site	Extraction method	No. m^{-2}	g m^{-2}	Reference
Arable land	Bardsey Island, U.K.	Handsorting	287	76	Reynoldson *et al.* (1955)
Arable land	Herts., U.K.	Formalin	18	1·6	Raw and Lofty (unpublished)
Arable land with dung	Herts., U.K.	Formalin	79	39·9	Raw and Lofty (unpublished)
Fallow soil	U.S.S.R.	Handsorting	18·5–33·5	4·6–8·4	Džangaliev and Belousova (1969)
Orchard with grass	Cambs., U.K.	Formalin and Handsorting	848	287	Raw (1959)
Orchard with grass	Holland	Handsorting	300–500	75–122	van Rhee and Nathans (1961)
Pasture	N. Wales	Handsorting	481–524	112–120	Reynoldson (1955)
Pasture	Westmorland, U.K.	Handsorting	389–470	52–110	Svendsen (1957)
Under pig litter	U.S.A.	Formalin	960	272	Edwards (unpublished)
Pseudotsuga mor	N. Wales	Handsorting	14·0	4·7	Reynoldson (1955)
Mixed woodland	N. Wales	Handsorting	157	40	Reynoldson (1955)
Quercus woodland	Hants., U.K.	Formalin	184	68	Edwards and Heath (unpublished)
Pinus woodland	Hants., U.K.	Formalin	40	17	Edwards and Heath (unpublished)

It seems likely that populations of non-lumbricid earthworms in the tropics and sub-tropics are smaller than lumbricid populations in temperate regions.

Enchytraeid worms attain their greatest density in acid soils with a high organic content, such as under coniferous forests and in moorland soils. In these habitats, where there are few lumbricid earthworms, enchytraeids play an increased role in litter fragmentation and breakdown.

IV. Role in Fragmentation and Incorporation

When litter is deposited on the soil surface, the first stage in its breakdown is fragmentation. For many types of deciduous forest litter, a period of "weathering" is required before fragmentation commences. In temperate regions, litter is fragmented mainly by earthworms, diplopods, isopods, dipterous larvae, Collembola and oribatid mites. Fragmentation is a very important stage in the process of decomposition, for if it is slowed down experimentally, then the whole process of decomposition is retarded. Witkamp and Crossley (1966) found that 45% of litter treated with napthalene to exclude most invertebrates broke down after one year, whereas in the same period 60% of litter decomposed in untreated soil.

Earthworms are important in this initial process of organic matter cycling, because certain lumbricids, in particular *L. terrestris*, seem to be responsible for the majority of litter fragmentation in woodlands and other tree-stand sites. Raw (1962) has shown that *L. terrestris* may remove more than 90% of the autumn leaf-fall in an apple orchard. In two woodland sites, earthworms consumed more *Fagus* (beech) and *Quercus* (oak) litter leaves than the rest of the soil invertebrates together (Edwards and Heath, 1963).

Soils with a low earthworm population often have a layer of undecomposed litter on the surface, with a sharp demarcation from the underlying soil, which usually has a poor crumb structure.

Figure 1 shows the weight of leaf material which became buried in relation to the weight of *L. terrestris* in *Malus sylvestris* Mill. (apple) orchards. The leaves were confined beneath wire mesh cages, each containing 100 or 200 leaves, and the *L. terrestris* population beneath each was estimated, using formalin. For a given weight of *L. terrestris*, more leaves were buried in arable than in grass orchards, probably because leaves lie directly on the bare soil in arable orchards, and are thus more directly available, and also because the leaves are the only form of litter present.

Edwards and Heath (1963) buried oak and beech leaf disks (cut from freshly fallen leaves) in nylon mesh bags in woodland and old pasture soil. They used four different size meshes, of which only the largest, of 7 mm aperture, would allow earthworms entry. After one year, none of the oak disks remained intact, 92% of the tota oak leaf material and 70% of the beech had been removed from the bags. Among other workers using similar techniques, von Perel *et al.* (1966) compared the disappearance of litter in 1 mm mesh nylon bags with that held under nylon net, but exposed beneath. They found that litter under the net disappeared 2–3 times faster than the litter in nylon bags and they concluded that earthworms were mainly responsible for this difference.

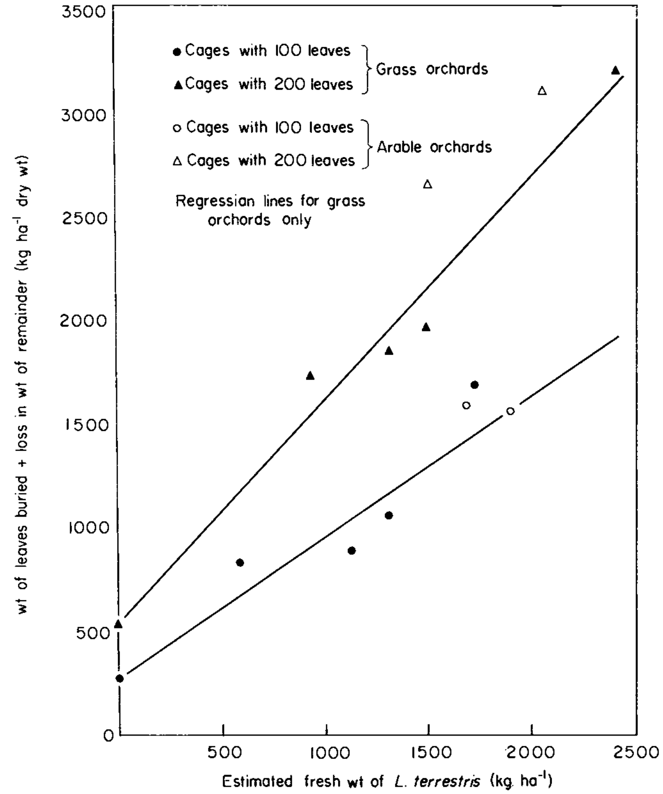

Fig. 1. Weight of leaf material buried in apple orchards in relation to the populations of *Lumbricus terrestris* in the soil.

A striking demonstration of the effectiveness of *L. terrestris* in fragmentation and incorporation of leaf litter has been provided by a comparison between the soil profile of a grass orchard (A) with a typical *L. terrestris* population, and an adjacent orchard (B) where *L. terrestris* was absent, and other species rare, due to long-term heavy spraying with a copper-based fungicide. The soil profile of orchard (A) had no litter accumulating on the surface, and the soil beneath possessed a well developed crumb structure, whereas that of orchard (B) had a surface mat, 1–4 cm thick, consisting of leaf litter in various stages of decomposition with the boundary between it and the soil beneath quite sharply defined (Fig. 2).

In New South Wales, pasture land deficient in earthworms also accumulated a similar layer up to 4 cm thick. When earthworms were introduced experimentally, this mat gradually disappeared. Grass plots on Park Grass, Rothamsted, that have very few earthworms because of regular treatment with sulphate of ammonia also have similar accumulations.

It is not only in deciduous woodlands and tree stands that earthworms are active. They also accelerate litter decomposition in coniferous woods. Heungens (1969) put individuals of *Dendrobaena octaedra*, *D. attemsi*, *D. rubida*, *Bimastos eiseni* and *Allolobophora chlorotica* (Sav.) into cultures of pine litter containing many needles. Initial fragmentation by the worms was indicated by a rapid decrease in volume of the culture material, as the size of the constituents decreased. After 3 months, the litter had been broken down into still smaller particles, and had decreased in volume by 13% in cultures with 2 worms per litre of litter, and by 26% when there were twelve worms per litre. The litter had also become mineralized to a certain extent. Further humification and mineralization processes were accelerated by the initial "macro-decomposition".

In contrast to the limited period of leaf fall in temperate woodlands, that of tropical and subtropical forests is continuous or nearly so. Where seasonal climatic changes occur, leaf fall is usually higher in the dry season. During the wet season, litter is fragmented and broken down by a variety of soil organisms, and decomposes very quickly, about 1% per day in West African forests (Madge, 1969), hence little or no litter accumulates (in temperate woodlands the rate is from 0·1 to 0·3% per day). There is little information on the ability of tropical earthworms to fragment and incorporate surface litter, and there seems no counterpart to *L. terrestris* in tropical regions. Many tropical earthworms are surface casting species, and as the amount of cast material is sometimes very great, these species may indirectly contribute to litter incorporation when the casts crumble in the dry season, burying litter in the process. Nye (1955) has reported that the material from casts decomposing during each dry season (mainly belonging to the eudrilid species *Hippopera nigeriae*) was sufficient to form a 1·3–2·5 cm layer of fine sandy loam over the soil surface.

Although enchytraeid worms are found in large numbers of plant litter, it is not easy to define their part in litter fragmentation. O'Connor (1957) suggested that many of the species present are in fact feeding on

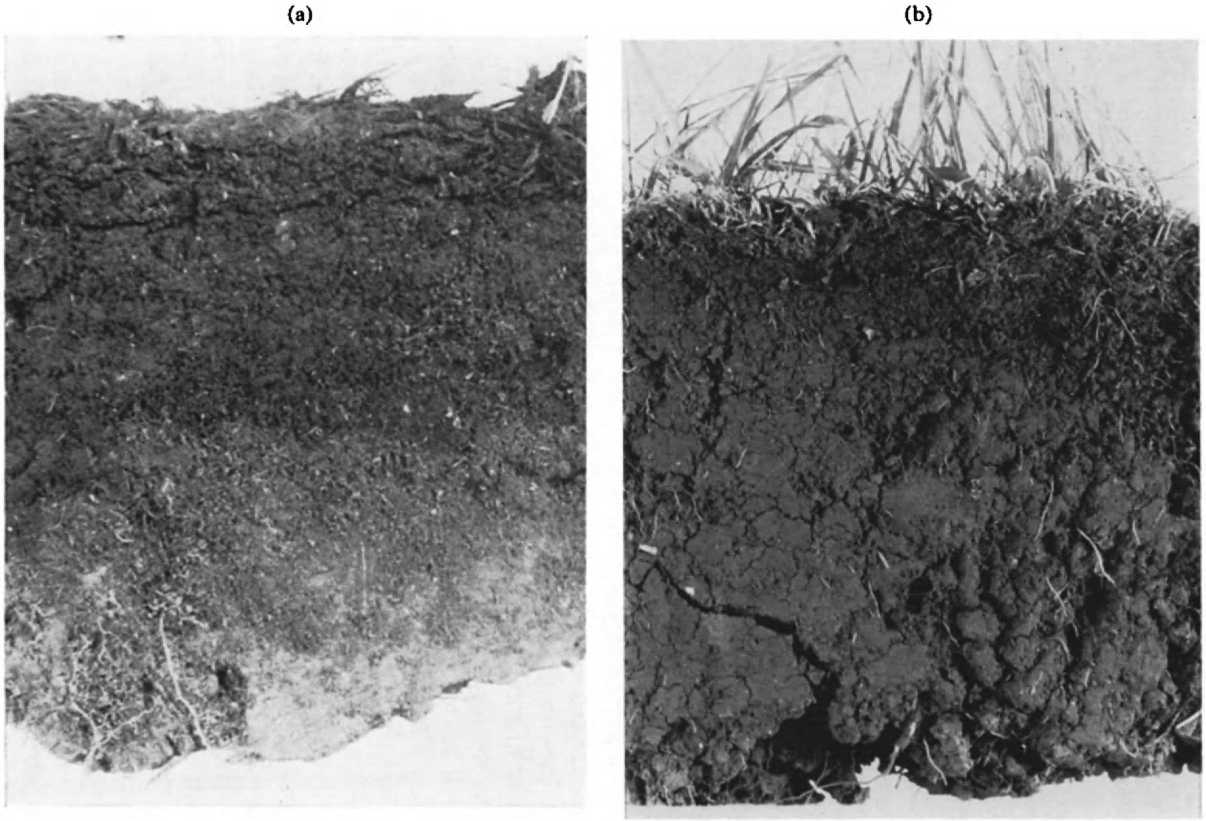

Fig. 2. Soil profile of a grass orchard. (a) No *Lumbricus terrestris*, showing surface matt of debris, (b) with a typical *L. terrestris* population.

fungi present in the litter layer. Nielson (1962) has found that at least some species do not possess the enzymes that would enable them to break down the complex higher plant polysaccharides which form the bulk of the litter layer. However, enchytraeids must be responsible for a certain amount of initial fragmentation, as they pass vegetable fragments through their guts.

Clark (1949) has reported that, in Australian forests, Enchytraeidae ingest fragmented plant material together with fungal mycelium, and Zachariae (1963) has stated that in both deciduous and coniferous woodlands, Enchytraeidae living in the litter layer consume loose particles of leaf material, together with Collembola frass.

V. Palatability of Different Types of Litter

Earthworms do not take different kinds of litter indiscriminately. Darwin and later workers have stated that they show a preference for leaves of different shapes. Many species of earthworms, including *Lumbricus terrestris*, *L. rubellus*, *Allolobophora caliginosa*, *A. rosea* (Sav.), *Eisenia foetida* and *Eiseniella tetaedra* (Sav.), are able to distinguish between different kinds of leaf litter (Lindquist, 1941). Bornebusch (1953) offered *L. terrestris* individuals a selection of leaves from a number of different plant species, including some herbaceous plants such as *Mercurialis perennis* L. (dog's mercury), deciduous trees, and some conifers. In general, the herbaceous plant leaves were preferred to deciduous tree leaves, and the latter to coniferous needles.

Many workers have shown that when earthworms are offered a choice of leaves all cut to a uniform size and shape, such as a disk, they still show a definite preference with the order of selection being little changed from that when the leaves are offered whole. The choice depends ultimately on the species to which the leaves belong, and the prior degree of weathering. Edwards and Heath (1963) buried 2·5 cm diameter leaf disks, taken from trees just before leaf fall, in nylon mesh bags with 7·0 mm apertures, in woodland soil. They found that *Quercus* leaves were taken in preference to *Fagus*. Heath *et al.* (1966), in a similar experiment using a range of leaves of different species, found that earthworms fed preferentially on *Ulmus* (elm), *Zea mays* (maize), *Betula* (birch), *Fraxinus* (ash), *Tilia* (lime), *Quercus* and *Fagus*, in that order (Fig. 3).

Many leaves become more palatable after a period of weathering on the ground, and the order of preference for weathered leaves may be different from that for leaves fresh from the tree. Thus, *L. terrestris* prefers fresh *Fagus* leaves to fresh *Malus sylvestris* leaves, but if the leaves have weathered for a few weeks, the preference is reversed.

The preference for some species of leaf is an indication of their relative palatibility. Although Gast (1937) attributed differences in palatability to variations in mineral content, this has not been subsequently confirmed. Sugar content, which has been correlated with protein content (Laverack, 1960) may be of importance, as protein-deficient litter is less readily acceptable than protein-rich litter. Leaves of *Mercurialis perennis*, *Urtica* sp. (nettle), *Sambucus nigra* (elderberry), *Fraxinus* and *Ulmus glabra* Huds. (wych elm), which are all particularly palatable to earthworms, contain no condensed tannins, whereas leaves of *Larix* (larch), *Picea* (spruce), *Quercus* and *Fagus*, all of which do, are very much less palatable (Brown *et al.*, 1963). King and Heath (1967) found that litter containing a high proportion of water-soluble polyphenols was consumed more slowly than litter with only a smaller proportion, and that, generally, litter became more palatable after some weeks of weathering, when much of the water soluble polyphenolic content had been leached out (see Williams and Gray, Chapter 19).

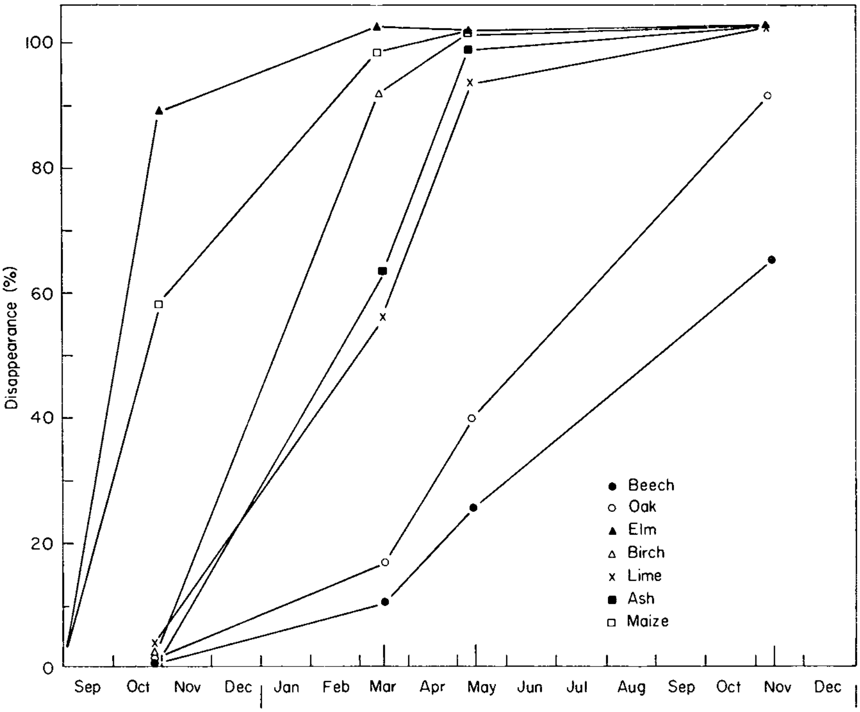

Fig. 3. Disappearance of leaf discs in 7 mm mesh bags in woodland soil (after Heath *et al.*, 1966).

In a comprehensive series of experiments Satchell and Lowe (1967) and Satchell (1967) found that amongst the factors that contribute towards litter palatability must be included nitrogen and carbohydrate content, and the presence or absence of a number of polyphenolic substances, particularly tannins.

VI. Role in Organic Matter Cycling

A. Consumption

Earthworms pass a mixture of organic and inorganic matter through their guts, the proportion depending upon the feeding and burrowing behaviour of different species. *Lumbricus terrestris*, a surface litter feeder, passes a high proportion of organic matter. Small species, such as *L. castaneus* (Sav.) and *Eisenia foetida*, living within the litter layer in woodlands, produce casts that often consist almost entirely of fragmented plant material. Species such as *Allolobophora longa*, *A. nocturna* and *A. caliginosa*, which live and, to a large extent, feed within the soil layers of woodlands and pastures, consume large quantities of mineral material when feeding. The casts of these species therefore contain a much smaller proportion of organic matter.

Satchell (1967) calculated that *L. terrestris* individuals consume 10% to 30% of their live weight (or about 100–120 mg) of plant litter per day, which compares with Needham's (1957) figure of 80 mg of *Ulmus* leaves per gram fresh weight of the species (8% of life weight) per day.

Many of the smaller species, e.g. *A. caliginosa*, *A. chlorotica* and *A. rosea*, can consume, weight for weight, similar quantities of litter material. However, the disappearance of litter due to these species is usually slower, as they tend to feed on the softer leaf tissues only, leaving the more lignified vascular tissues (van Rhee, 1963).

B. Turnover

Guild (1955) fed three species of lumbricid earthworms, *A. caliginosa*, *A. longa*, and *L. rubellus*, on cow dung for two years. During this period, individuals consumed 35–40 g, 20–24 g and 10–20 g respectively, equivalent to an annual consumption of 17–20 t of dung per ha by a field population of 120,000 adults per ha. Raw (1962) reported that, in an arable orchard, a *L. terrestris* population consumed over 93% of the annual leaf-fall (2000 kg of leaf litter per ha) between October and the end of the following February.

These observations show that earthworms are capable of consuming (or removing from the surface) a considerable proportion of the plant debris that is produced annually in various ecosystems.

The weight of annual leaf-fall in woodlands and forests varies considerably depending on the climatic zone within which they occur. Thus temperate deciduous forests produce 2·5–3·5 t ha^{-1} year, tropical forests 5·5–15 t, and arctic forests as little as 0·5 t ha^{-1} year. Satchell (1967) has calculated that the earthworm population could consume the entire leaf-fall of a temperate deciduous woodland, assuming an annual leaf-fall of 3 t ha^{-1}, and the consumption of 27 mg g^{-1} of leaf litter per day by the earthworms.

One of the major factors in litter destruction by earthworms is the amount of organic material available to them. In an experiment where mesh cages containing leaves were put down in apple orchards, *L. terrestris* removed more leaves from cages with 200 leaves than from those with half this number (Raw, 1962) (Fig. 1). It seems likely that, provided the soil conditions are optimum, numbers of earthworms will increase until the amount of food material available becomes the limiting factor.

C. Humification

After fragmentation and incorporation within the soil, the final process of plant litter breakdown is humification. This is the final breakdown into a complex stable product consisting of an amorphous colloidal substance containing a number of phenolic substances.

Much of the final decomposition is brought about by the direct action of microflora in the lower soil layers. This activity increases during the autumn in temperate areas. Other small organisms that contribute to humification are the small arthropods such as mites and springtails. The role of the earthworm is not clear. Some contribution must come from the action of microflora in the earthworm's gut, and the process is continued in cast material. Earthworm casts have been shown to contain larger populations of micro-organisms than the surrounding soil (Stöckli,1928; Ponomareva, 1962; Zrazhevskii, 1957). Another contribution is that of combining fragmented organic matter with soil taken in with food—thus completing incorporation of the organic matter with soil, and thereby enhancing the effect of microfloral action.

D. Energetics

Satchell (1967) has calculated the oxygen consumption of a *L. terrestris* population of a *Fraxinus–Quercus* wood, with a biomass of 140 g m^{-2} to be about 22·9 l m^{-2}, an energy of respiration equivalent to 110 kcal m^{-2} per annum, and about 8% of the total energy content of the annual leaf fall.

Barley and Kleinig (1964), working from the oxygen consumption of *A. caliginosa* individuals in a respirometer, calculated that a population of this species in a pasture, with a biomass of 80 g m^{-2}, would contribute only about 4% of the total annual energy of decay of the organic matter present.

O'Connor (1963) estimated the energy of respiration of an enchytraeid population in a douglas fir plantation to be 150 kcal m^{-2}, 11% of the total energy content of the annual litter fall.

There is no information on the direct contribution to soil metabolism by tropical and sub-tropical oligochaetes; however, there is no reason to suppose that it is any greater than that of temperate oligochaetes.

The direct contribution to soil metabolism by the Oligochaeta may therefore be considered to be much less than the contribution by other soil animal groups taken together.

VII. Nitrogen Mineralization

Up to 72% of the dry weight of earthworms is protein (Lawrence and Millar, 1945) which indicates that on their death earthworms are a valuable source of nitrogen which is being returned continuously to the soil. Satchell (1967) calculated the weight of earthworm tissue produced by a *L. terrestris* population in a *Fraxinus–Quercus* wood at about 364 g m^{-2}. Working on the basis that the nitrogen content of *L. terrestris* is about 1·75% of fresh weight, he estimated the amount of nitrogen returned to the soil annually from worms dying in this population to be 6–7 g m^{-2}.

After death, earthworms decay rapidly in most soils, disappearing completely after 2–3 weeks. About 25% of the nitrogen from decomposing worms is in the form of nitrate and 45% as ammonia, with the remainder as soluble organic matter in components such as setae and cuticle.

Mineralizable nitrogen is also produced by living earthworms in their excreta, since they consume large quantities of plant material, which itself is a considerable source of nitrogen. Of the total nitrogen excreted by worms about half is secreted by gland cells in the epidermis as mucoproteins, and half excreted from the nephridiopores as ammonia, urea, allantoin and uric acid.

Barley and Jennings (1959) found that when non-available nitrogen, in the form of fragmented plant litter, was fed to immature individuals of *A. caliginosa*, about 6% was excreted as available nitrogen. Needham (1957) has provided data on the rate of nitrogen excretion by earthworms. His figure for *L. terrestris* was 269 μg g^{-1} day at 23°C. Needham considered that very little nitrogen is excreted in the faeces, although other workers, notably Lunt and Jacobsen (1944) and Graff (1972), have found that earthworm casts contain considerably more nitrogen than the surrounding soil. Using Needham's figures Satchell (1967) estimated the amount of nitrogen excreted annually by earthworms in the oak/ash wood previously referred to, and calculated the total annual yield of nitrogen both from the excreta of the population and from dead worms to be about 100 kg ha^{-1}.

VIII. Effects on the C:N Ratio

Unless the ratio of carbon to nitrogen (C:N ratio) in organic matter is less than 20:1, plants are unable to assimilate the unchanged nitrogen. Freshly fallen leaves have a much higher ratio than this; *Ulmus* leaves 24·9:1, *Fraxinus* 27·6:1, *Tilia* 38·2:1, *Quercus* 42·0:1, *Betula* 43·5:1, *Sorbus aucuparia* L. 54·0:1 and *Pinus sylvestris* L. 90·6:1 (Wittich, 1953). Often the C:N ratio of plant material is correlated with the degree of palatability to earthworms. Soft, succulent leaf tissues frequently have comparatively low C:N ratios, whereas the more initially unpalatable, tough tree leaves that have a high percentage of cellulose and lignin often have high C:N ratios. This means that large amounts of nitrogen in litter remain unavailable to plants until such time as the C:N ratio is reduced to below 20:1. Many of the tougher, less palatable tree leaves (with the higher C:N ratios) have to undergo a period of weathering before they become acceptable to earthworms. Once earthworms begin to feed on plant litter, they gradually reduce its C:N ratio. The extent to which they lower the C:N ratio of their food material can be judged by the amount of carbon assimilated, which in turn can be assessed approximately by measuring their respiration. This is not a particularly accurate method, as earthworm respiration can be affected by many factors. However, Barley and Kleinig (1964) calculated that a population of *A. caliginosa* accounted for only 4% of the total carbon consumption, and Satchell (1967) calculated a comparable figure of 8% for *L. terrestris* in two English woodlands. These rates of carbon consumption are too small to reduce the C:N ratio of most litter to a level at which nitrogen is available to plants. The earthworms were inactive when the measurements were made, so the estimates are probably too low, and Satchell considered that a more accurate figure for the carbon respired by earthworms would be 12% of that consumed. Satchell estimated that in one of his woodland sites, the C:N ratio of the litter was 385. Even using his revised carbon respiration estimate this would only lower the C:N ratio to about 33·5. Satchell suggested, therefore, that other groups of animals, such as nematodes, have a smaller biomass but have a higher metabolic rate and may play a more important role in affecting the C:N ratio of litter.

IX. Effect on Available Mineral Nutrients

Many workers have analysed earthworm casts, and soil with and without earthworms, for available mineral elements, and have reported that earthworm casts have higher concentrations of these than associated soils. This has been demonstrated by Lunt and Jacobson (1944) (Table II), Nijhawan and Kanwar (1952) in India, and Nye (1955) in Nigeria. Soils containing a large population of earthworms are also reported to have more exchangeable calcium, magnesium and potassium and available phosphorus than soils with few or no earthworms (Stöckli, 1949; Ponomareva, 1950; Nye, 1955). It has been reported from New Zealand that when European earthworm species were introduced into pastures that were poor in available molybdenum, although rich in total molybdenum, they greatly increased the supply of the element available to plants. Graff (1972) has reported that earthworms were responsible for a large increase in amount of available nitrogen, phosphorus and potassium in brown earth soil.

TABLE II. Comparison between available mineral elements in earthworm casts and ploughed soil

In ppm	Earthworm casts	0–15 cm soil layer
Nitrogen (nitrate)	21·9	4·7
Calcium (exchangeable)	2793	1993
Magnesium (exchangeable)	492	162
Phosphorus (available)	150	20·8
Potassium (available)	358	32·0

Adapted from Lunt and Jacobson (1944).

It seems to be generally agreed from all the evidence available that the presence of earthworms and their faecal material are responsible for increasing the proportions of soil minerals which are available to plants.

X. Effects of Earthworms on Soil Micro-organisms

The alimentary canal of earthworms contains many species of micro-organisms. Most workers are agreed that these species are the same as those found in the soil from which the worms have been taken. Bassalik (1913) was the first to isolate micro-organisms from earthworms, and he found more than 50 species of bacteria in the gut of *Lumbricus terrestris*, which were also present in the soil in which the worms lived. This finding has been confirmed by Parle (1963) and Satchell (1967), who also concurred with this view, and concluded that earthworms are unlikely to possess an indigenous microfloral population in their guts.

There is, however, much evidence to show that numbers of micro-organisms can greatly increase in earthworm guts compared with the numbers in surrounding soil (Stöckli, 1928; Ponomareva, 1953). The greatest numbers are found in the more posterior parts of the gut (Parle, 1959) (Table III).

It is therefore to be expected that earthworm casts will contain many more micro-organisms than will the associated soil. This has been confirmed by Ponomareva (1962), who found 13 times more bacteria in earthworm casts than in the surrounding soil. Ghilarov (1963), Zrazhevskii (1957), Went (1963), Dawson (1948) and Teotia (1950) have all reported larger microfloral populations in cast material than in surrounding soil. The casts are therefore foci from which soil micro-organisms can spread into surrounding soil. Koylovskaya and Zhdannikova (1961) compared the microfloral populations of the gut contents of two lumbricid species living at different soil depths. They found that *L. rubellus*, which lives in the top 5 cm of soil, had more than ten times the numbers of bacteria in its gut compared with the soil in which it lives, whereas *Octolasium lacteum* which lives at between 10 and 40 cm, had a bacterial population in its gut which was little, if at all, greater than in the soil. However, the casts of both species contained proportionately more fungi, actinomycetes and cellulose-decomposing and butyric acid-forming bacteria than the surrounding soil. Organic matter decomposed much faster in the casts of these two species than in the soil.

TABLE III. Numbers of micro-organisms in the fore-, mid- and hind-gut of *L. terrestris* ($\times 10^6$)

	Fore gut	Mid-gut	Hind-gut
Actinomycetes	26	358	15,000
Bacteria	475	32,900	440,700

Data from Parle (1959).

Differences in microbial populations in earthworm casts and surrounding soil are due either to environmental changes within the earthworm's gut or to the food material ingested which provides a rich substrate, thereby increasing microfloral activity. Which of these is the major factor is debatable; certainly the type and quality of ingested material helps determine the size of microfloral populations in casts, but, as Parle (1959) showed, numbers of bacteria and actinomycetes in ingested material increased by a factor of 1000 while passing through the earthworm's intestine, and microbial activity in the casts was still much greater than in the surrounding soil 50 days after their excretion.

Tenney and Waksman (1929) and Harmsen and van Schreven (1955) have reported that when simple nitrogenous compounds are added to soil, then the decomposition of the organic matter it contains is accelerated (particularly if the organic matter is already poor in nitrogen). Therefore, since earthworm casts are usually rich in nitrogenous compounds, the presence of earthworms may help to stimulate microbial decomposition of organic matter in the soil. Barley and Jennings (1959) added grass, clover litter and dung pellets to soil cultures containing populations of *Allolobophora caliginosa* equivalent to those found in the field, and to soil cultures without earthworms. They found that the rate of litter decomposition (estimated by the accumulation of nitrate and ammonia) was 17–20% greater in the cultures with earthworms. They estimated that half of the increased rate of decomposition was due directly to the earthworms, and half to the increase in microbial activity induced by the worm's excretory products.

XI. Influence of Environmental Factors on Litter Breakdown by Earthworms

A. Soil Type

Numbers of earthworms and the population composition are much influenced by soil type (Table IV). Light and medium loams have a higher population than heavy clay soils and alluvial soils. Acid peaty soils have a much reduced population, and also fewer species. In England *L. terrestris*

TABLE IV. Relation of soil type to earthworm populations

Soil type	Population	
	Number per ha	Number of species
Light sandy	57	10
Gravelly loam	36	9
Light loam	63	8
Medium loam	56	9
Clay	40	9
Alluvium	44	9
Peaty acid soil	14	6
Shallow acid peat	6	5

From Guild, 1951.

is most abundant in light loamy soils. *A. caliginosa* is the commonest species in all but the acid peaty soils, in which *Bimastos eiseni* and *Dendrobaena octaedra* (both small species feeding in the surface mat) are most commonly found. The greatest diversity of species in temperate areas is found in mull soils. Satchell (1967) reported eight characteristic species, including *L. terrestris*, *A. longa* and *A. caliginosa*, from mull sites in the English Lake District. In moder sites, there were usually only four species of small size, of which the largest was *L. rubellus* a humus and surface mat feeding species, which was much less abundant than in the mull sites. In the most extreme acid mor sites, only two species, *D. octaedra* and *B. eiseni*, were found. However, although mor soils contain few species of small biomass, whose contribution towards litter incorporation is comparatively small, other faunal groups, including considerable populations of many species of enchytraeids, are found in these sites. Layers of unincorporated organic matter persist in these sites despite the presence of earthworms, enchytraeids, microarthropods and the associated microflora. Handley (1954) has suggested that organic nitrogenous material in mor sites is not so easily digestible as is that in mull.

B. Effects of Temperature

Most species of earthworms in the temperate zones are most active during the spring and autumn months. During the summer and winter months their activity is much reduced or ceases temporarily, depending on the species. During the summer months some, such as *Allolobophora longa*, go into an obligatory diapause when soils become dryer. Others, such as *L. terrestris*, retreat deeper into their burrows, and feed less. During winter, as the soil becomes colder, most species retreat deeper into the soil; feeding and other activities become minimal. *L. terrestris* ceases to feed on the surface when the temperature of the soil surface approaches 0°C. Table V gives the results obtained when cultures of *L. terrestris*, provided with apple leaves as food, were exposed to four different temperatures for a period of four months.

Although worms kept at 15°C buried most leaves during the first month, the rate was much reduced during the remainder of the period. Over the whole period, most leaves were buried by worms kept at 10°C. Kollmannsperger (1955) noted a positive correlation between the number of earthworms on the soil surface at night and temperature; 10·5°C being the optimum temperature for activity. Satchell (1967) concluded that earthworms were most active on the soil surface, when temperatures at night were not less than 10·5°C, provided the grass–air temperature was above 2°C, and the soil surface was moist from recent rain.

TABLE V. Effects of temperature on leaf burial. Number of leaves buried by 2 *L. terrestris* at different temperatures in four successive months.

	0°C	5°C	10°C	15°C
After 1 month	0	25	35	67
After 2 months	0	33	31	30
After 3 months	0	53	63	33
After 4 months	0	67	75	44
	0	178	204	174

From Lofty unpublished.

XII. Conclusion

The major contributions by oligochaetes to plant litter breakdown can be summarized by the following stages:

1. *The removal of leaf and other litter material from the soil surface.* This is achieved by the lumbricid earthworm *Lumbricus terrestris* in temperate regions, particularly in deciduous tree stands on mull soils, where a population is capable of removing up to 90% of a seasons leaf fall annually, and is of great importance in initiating the process of plant litter decay.

2. *Litter burial.* Many species of earthworms cast on the surface, and this cast material contributes to litter burial, bringing the litter into greater contact with other plant material decomposers. In tropical and subtropical soils, where earthworms otherwise play a much smaller part in litter decomposition than they do in temperate regions, some species produce surface casts to such an extent that, in certain areas, they will form, on breaking down, a layer up to 4 cm deep over the surface.

3. *Fragmentation.* When feeding on plant remains, oligochaetes, particularly *L. terrestris* and those earthworms and Enchytraeidae living in litter layers, fragment the material, greatly increasing the surface area on which other decomposers may feed.

4. *Incorporation.* Of considerable importance is the action of earthworms in incorporating fragmented and decomposed plant material throughout the soil horizons within which they live, by their burrowing activities. Cast material is either deposited freely in the soil, or forms a lining of the burrows. Mor type soils, with few earthworms, have a mat of slowly decomposing plant material on the surface, showing no incorporation with the soil layers below.

5. *Effect on the C:N ratio.* During its passage through the guts of earthworms, the ratio of carbon to nitrogen in the ingested plant material is

reduced towards the level at which the material can be directly assimulated by plants.

6. *Effects on the soil microflora.* Earthworm faeces (cast material) are much richer in numbers of microflora than the surrounding soil, many of which are involved in the final humification of plant material in the soil.

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